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RESEARCH ARTICLE

Pleistocene fossils from Japan show that the recently extinct Spectacled Cormorant (*Phalacrocorax perspicillatus*) was a relict

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ABSTRACT

Despite increasing attention to geologically recent extinctions in the ocean, little information is available on natural distributions of extinct species before contact with humans. In the North Pacific, a large cormorant, *Phalacrocorax perspicillatus* (Spectacled/Pallas's Cormorant), was driven to extinction in the 19th century, probably due to overexploitation by humans. So far, no clear evidence has existed for the past presence of the cormorant species outside Bering Island, Commander Islands. We report fossil remains of *P. perspicillatus* from the upper Pleistocene (Marine Isotope Stage 5e, ~120,000 yr ago) of Shiriya, northeast Japan. The occurrence is the first definitive record of the species outside Bering Island, and the first pre-Holocene record for the species, expanding the known geographic and temporal ranges of the species by ~2,400 km and ~120,000 yr, respectively. It indicates that the species had undergone a drastic range contraction or shift since the Pleistocene, probably before the first contact with humans. Available evidence indicates a drop of oceanic productivity near Shiriya in the Last Glacial Maximum (~17,000 yr ago), which might have affected the local population of the cormorant species and possibly led to the species' local disappearance from this area. In any case, the population of *P. perspicillatus* on Bering Island at its first scientific discovery should be considered a relict.

Keywords: biogeography, extinction, fossil birds, Phalacrocoracidae, *Phalacrocorax perspicillatus*, Pleistocene

Fósiles del Pleistoceno de Japón muestran que la especie *Phalacrocorax perspicillatus* recientemente extinta era un relicto

RESUMEN

A pesar de la mayor atención a las extinciones recientes en términos geológicos en el océano, hay poca información disponible sobre las distribuciones naturales de especies extintas antes del contacto con los humanos. En el Pacífico del Norte, una especie de cormorán grande *Phalacrocorax perspicillatus* fue llevada a la extinción en el siglo 19, probablemente debido a la sobreexplotación por parte de los humanos. Hasta ahora, no ha existido información clara de la presencia pasada de esta especie de cormorán afuera de la Isla de Bering, Islas Commander. Aquí, brindamos información sobre restos fósiles de *P. perspicillatus* provenientes de Pleistoceno tardío (Etapa de Isótopo Marino 5e, ~120,000 años atrás) de Shiriya, en el noroeste de Japón. Esta presencia es el primer registro definitivo de la especie afuera de la Isla de Bering, y el primer registro antes de Holoceno para la especie, expandiendo los rangos geográfico y temporal conocidos de la especie en ~2400 km y ~120,000 años, respectivamente. Esto indica que la especie había experimentado una drástica contracción o desplazamiento del rango desde el Pleistoceno, probablemente antes del contacto con los humanos. La evidencia disponible indica una caída de la productividad del océano cerca de Shiriya en el Último Máximo Glaciar (~17,000 años atrás), lo que podría haber afectado a la población local de esta especie de cormorán y posiblemente haber ocasionado la desaparición local de la especie en esta área. En cualquier caso, la población de *P. perspicillatus* en la Isla de Bering a partir de su primer descubrimiento científico, debería ser considerada como un relicto.

Palabras clave: aves fósiles, biogeografía, extinción, Phalacrocoracidae, *Phalacrocorax perspicillatus*, Pleistoceno

INTRODUCTION

Extinction in geologically recent time has been subject to intensive scientific inquiries, in connection to impacts of human activity and climate change, as well as to their ecological consequences (Koch and Barnosky 2006, Dirzo et al. 2014, Galetti et al. 2018). Although relatively poorly understood compared to terrestrial extinctions, recent extinctions in the marine ecosystem are gaining increasing attention in the past few decades (Carlton et al. 1999,

McCauley et al. 2015, Estes et al. 2016). In order to correctly appreciate the impact of human activity on those extinctions, it is imperative to accurately assess natural distributions of extinct animals before or at the time of first contact with humans, for which fossil and archeological remains play crucial roles (Lotze and Worm 2009, Crerar et al. 2014).

One of the most famous examples of extinction in the ocean is that of *Pinguinus impennis* (Great Auk), a flightless seabird that was once widespread in the North Atlantic but was driven to extinction in the mid-19th century due to overexploitation by humans (Fuller 2001, Hume and Walters 2012). One potential parallel is known from the North Pacific: *Phalacrocorax perspicillatus* (Spectacled/Pallas's Cormorant), a large cormorant that also became extinct in the mid-19th century (Stejneger 1883, 1885). The cormorant was first discovered on Bering Island, Commander Islands (55°N, 166°E), in the 18th century by the explorer Georg Steller, who eventually became the only naturalist to report the bird in life, and it was scientifically described in the early 19th century on the basis of his report (Pallas 1811). It was the largest living member of the cormorant family (Johnsgard 1993) and is sometimes considered an example of island gigantism (Palmgren 1935). Although the species is generally considered a reluctant flyer, its morphology indicates that it was capable of flight (Stegmann 1936, Livezey 1992). Stejneger's expedition in 1882 confirmed that the species had not been seen by local people for ~30 yr; thus, it had probably become extinct around that time (Stejneger 1883). It is commonly thought that the primary cause of its extinction was overexploitation by humans on the island (Stejneger 1883, Greenway 1967), although suggested causes of decline include destruction of breeding grounds by volcanic eruptions (Stejneger and Lucas 1889) and an epidemic of disease (Hartert 1920).

A single archeological specimen from Amchitka Island, in the Aleutians, was identified as *P. perspicillatus* by Siegel-Causey et al. (1991), but Olson (2005) later showed that the specimen falls within the variation of a modern North American species, *P. auritus* (Double-crested Cormorant), pointing out the large size of *P. auritus* near that region (subspecies *cincinatus*). As such, there has been no definite record of this species outside Bering Island, although Stejneger and Lucas (1889) speculated that it may have occurred on other islands in the region as well.

Here, we report the first definitive fossil record of *P. perspicillatus* from Shiriya, northeast Japan (41.4°N, 141.4°E; Figure 1). Fissure-filling deposits in Shiriya are known to yield a Middle–Late Pleistocene vertebrate assemblage consisting of various land and marine vertebrates (Hasegawa et al. 1988). Two cormorant bones from the deposits have been identified as *P. filamentosus* [= *capillatus*] (Japanese Cormorant) by Hasegawa et al. (1988). These specimens and some other cormorant bones from the deposits, however, are in fact much larger than modern *P. capillatus* and *P. carbo* (Great Cormorant), which are among the largest living cormorant species, and turned out to represent an extralimital species, *P. perspicillatus* (Figure 2).

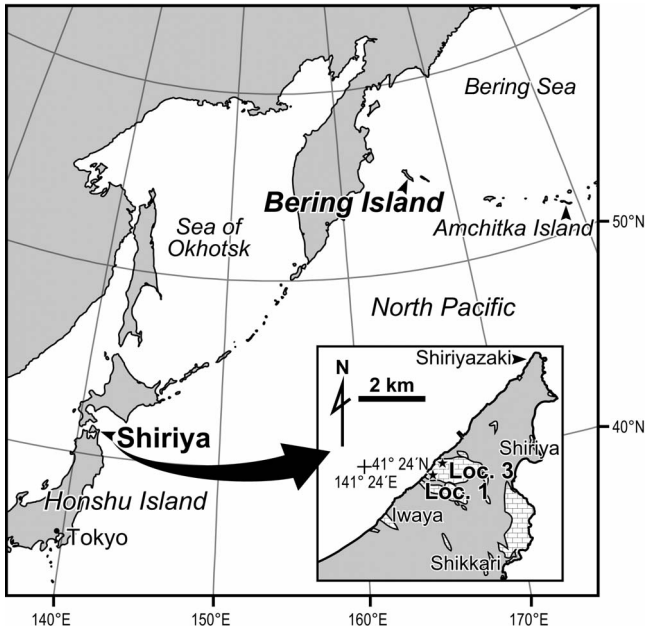

FIGURE 1. Geographic locations of Shiriya and Bering Island. (Inset) Exact locations of fossil localities (stars; after Hasegawa et al. 1988); distribution of limestone is indicated by the brick pattern (after Tsushima and Takizawa 1977).

MATERIAL AND METHODS

Institutional Abbreviations

EP = Masaki Eda Collection, Hokkaido University Museum, Sapporo, Japan; KUGM = Department of Geology and Mineralogy, Kyoto University, Kyoto, Japan; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA; NSMT AS and PV = Avian Skeleton Collection, Department of Zoology, and Vertebrate Paleontology Collection, Department of Geology and Paleontology, respectively, National Museum of Nature and Science, Tsukuba, Japan; USNM O and PV = Division of Birds, Department of Vertebrate Zoology, and Vertebrate Paleontology Collection, Department of Paleobiology, respectively, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UWBM = Ornithology Collection, Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA; and YIO = Yamashina Institute for Ornithology, Abiko, Japan.

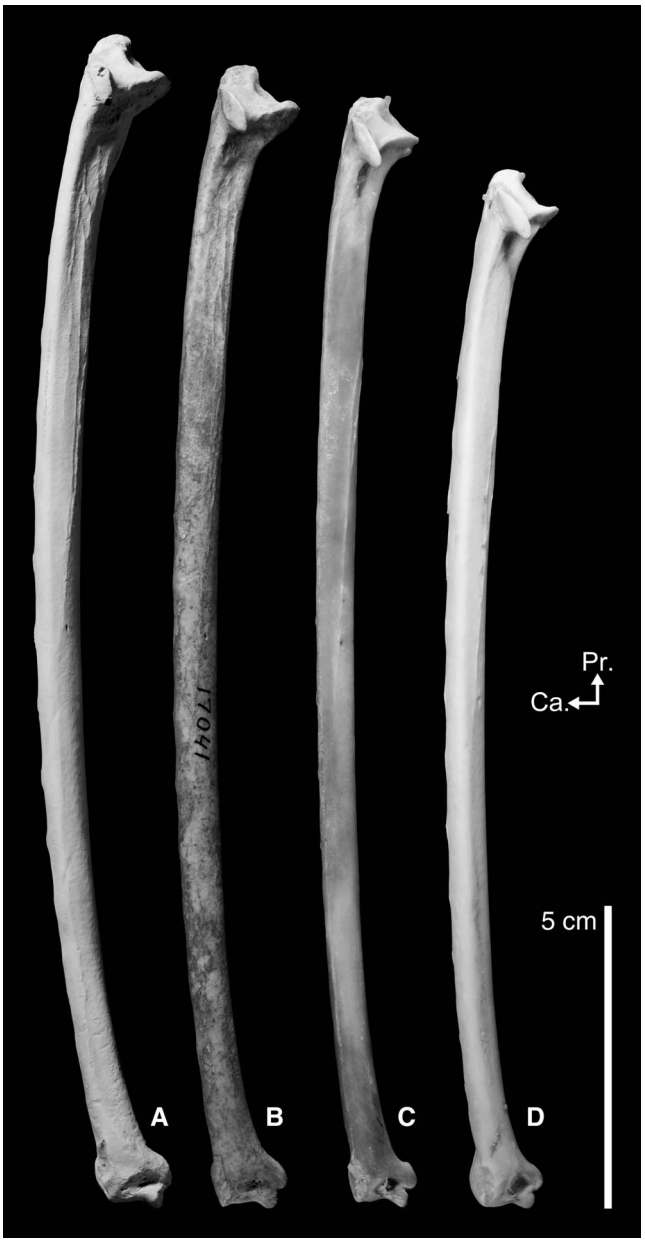

FIGURE 2. Ulna of *Phalacrocorax perspicillatus* from Shiriya compared with those of *P. perspicillatus* from Bering Island and large individuals of other species. Each is a right ulna in dorsal view. (**A**) *P. perspicillatus* from Shiriya (NSMT PV 24191). (**B**) *P. perspicillatus* from Bering Island (USNM O 17041). (**C**) Modern *P. carbo sinensis* (USNM O 29696). (**D**) Modern *P. auritus* (USNM O 499388). Arrows denote anatomical orientation. Shiriya fossil is coated with ammonium chloride. Abbreviations: Ca. = caudal; Pr. = proximal.

Fossil Localities

The fossils described here came from Pleistocene deposits in Shiriya, which is located at the northeastern extremity of Honshu Island, Japan (Figure 1). The geology of the fossil localities was detailed elsewhere (Hasegawa et al. 1988, Watanabe and Matsuoka 2015). Vertebrate fossils in this area occur from unconsolidated deposits that fill fissures and caves developed in pre-Tertiary limestone bodies (Tsushima and Takizawa 1977, Hasegawa et al. 1988). Among the 4 vertebrate localities recognized by Hasegawa et al. (1988), Loc. 1 and Loc. 3 yielded the fossils described here. The cormorant fossils co-occur with various vertebrate remains, including land and marine mammals, birds, amphibians, and fish (Hasegawa et al. 1988). The avian material is currently under revision by the authors (Watanabe and Matsuoka 2015, Watanabe et al. 2016).

Although no direct dating is available for the fossil localities, the occurrence of marine vertebrates and inclusion of marine-originated sediments indicate that the fossil-bearing layers had been deposited near the past sea level, after which local uplift and eustatic sea-level changes took place (Hasegawa et al. 1988). Therefore, the localities can be correlated to marine terraces developed in this area, each of which can be assigned to a certain Marine Isotope Stage (MIS) based on dated volcanic ash layers interbedded within its deposits and relative altitude to others (see Hasegawa et al. 1988, Watanabe and Matsuoka 2015); both Loc. 1 (~45 m above sea level) and Loc. 3 (~35 m a.s.l.) can be correlated to MIS 5e (~120,000 yr ago or the Last Interglacial; age of marine terraces follows Koike and Machida 2001). The marine-terrace-based age correlation is consistent with the occurrence of land mammals typical of the Late Pleistocene of Japan (Hasegawa 1972, Kamei et al. 1988).

Late Pleistocene oceanographic conditions around Shiriya have been reconstructed from radiolarian assemblages from a seafloor sediment core (Matsuzaki et al. 2014); it has been shown that the age of the Shiriya local fauna, MIS 9–5e, was characterized by higher sea surface temperature and raised oceanic productivity than the preceding period. Although little information is available for the Pleistocene terrestrial paleoclimate around Shiriya (northern Honshu), palynological analyses of lacustrine sediment cores in central Honshu gave some ideas; the paleoclimate in MIS 5e was slightly or considerably cooler than today, with the amount of precipitation being of similar order (Tarasov et al. 2011, Kigoshi et al. 2017).

Fossil Material

Most of the fossils were collected at Loc. 3 by Y. Hasegawa and colleagues in the 1960s or in 1987; and some others at Loc. 1 were collected by Z. Nakajima in the 1950s. Exact collection localities were not recorded for the other few specimens. All specimens described here are now formally deposited at NSMT PV. All the limb bones described are skeletally mature, as confirmed by the smooth surface texture that is observed after the cessation of active bone growth (Tumarkin-Deratzian et al. 2006, Watanabe and Matsuoka 2013, Watanabe 2018).

Comparative Material, Terminology, and Measurement

Comparison was primarily done with modern avian skeletons stored in EP, KUGM, MVZ, NSMT AS, UWBM, USNM O, and YIO. Comparison with *Phalacrocorax perspicillatus* was based on a composite assemblage of subfossil bones from Bering Island (USNM O 17041 and 19417; Stejneger and Lucas 1889). Classification of the family Phalacrocoracidae Reichenbach, 1849–1850 (1836) is rather versatile (Siegel-Causey 1988, Johnsgard 1993, Kennedy and Spencer 2014); thus, all modern species are treated here under a single genus, *Phalacrocorax* Brisson, 1760, for convenience. Comparison with selected fossil species was made mainly on the basis of published descriptions. Although comparison was made with as many species as possible, only North Pacific species are mentioned in the text for brevity. A list of comparative material is given in Appendix A.

Osteological terminology generally follows Baumel and Witmer (1993), but that of Howard (1929) is also used when appropriate. Measurements were taken with digital calipers (Mitutoyo, Kawasaki, Japan) and values rounded to the nearest 0.1 mm are reported. For wing elements, "width" stands for dorsoventral width or diameter, and "depth" for craniocaudal depth or diameter. For other elements, "width" stands for mediolateral width, and "depth" is taken perpendicularly to width.

SYSTEMATIC PALEONTOLOGY

Family **Phalacrocoracidae** Reichenbach, 1849–1850 (1836)
Genus ***Phalacrocorax*** Brisson, 1760
Phalacrocorax perspicillatus Pallas, 1811
(Figures 2A, 3A–3G, 3K–3P, 4A, 4E, 4I)

[1988 *Phalacrocorax filamentosus* (Temminck and Schlegel); Hasegawa et al.: pl. 7, figs. 3, 4]

Material. Loc. 1: right omal coracoids, NSMT PV 24186 and 24187; left distal humerus, NSMT PV 24188; left tarsometatarsal shaft, NSMT PV 24189. Loc. 3: left quadrate lacking processus orbitalis, NSMT PV 24190; left distal humerus, NSMT PV 19000; complete right ulna, NSMT PV 24191; left distal radius, NSMT PV 19001; pelvic fragment around left acetabulum, NSMT PV 24192; left distal tibiotarsus, NSMT PV 24193. Locality unknown: left caudal pterygoid, NSMT PV 24194; right proximal radius, NSMT PV 24195; left femoral shaft, NSMT PV 24196. All specimens were recovered as isolated bones; thus, possible associations between specimens are uncertain.

Locality and age. Two fissure-filling deposits in Shiriya, Aomori Prefecture, Japan (Loc. 1 and 3 of Hasegawa et al. 1988), 41.4°N, 141.4°E. Probably Late Pleistocene (Marine Isotope Stage [MIS] 5e) in age, based on correlation to marine terraces.

Measurement. See Table 1 and Figure 5.

Description and comparison. Two specimens preserving omal ("upper" or "shoulder") parts of the coracoid are referred to this species (Figure 3E–3G). The Shiriya coracoids are far larger than the coracoids of *P. pelagicus*, *P. urile*, and *P. penicillatus*, and comparable in size to subfossil bones of *P. perspicillatus* from Bering Island and to the largest individuals of *P. carbo*, *P. capillatus*, and *P. auritus* (Table 1 and Figure 5A). The Shiriya coracoids agree with the former and differ from the latter in the following features: (1) the facies articularis clavicularis is strongly expanded medially from the ventromedial margin of shaft as in *P. pelagicus* and *P. urile* (Figure 3E, 3F); (2) the area on the ventral surface of the processus acrocoracoideus lateral to the facies articularis clavicularis is rather narrow, a feature otherwise unique to *P. penicillatus*; (3) the profile of the tuberculum brachiale is straight in medial view, rather than being convex as in *P. carbo* and *P. capillatus* (Figure 3G–3J); and (4) the omal part of the sulcus supracoracoideus is deeply excavated, with the tuberculum brachiale overhanging as in *P. pelagicus* and *P. urile* (Figure 3G, 3H).

Two moderately worn distal humeri are referred to this species (Figure 4A, 4E, 4I). Their size falls within the ranges of *P. perspicillatus* and large individuals of *P. carbo* and *P. auritus* (Table 1 and Figure 5B). The Shiriya humeri agree with the humerus of *P. perspicillatus* from Bering Island in the following features, which are unique among the species examined: (1) a rather bulbous condylus ventralis that is developed as distally as the level of the distal margins of the processus flexorius and condylus dorsalis (Figure 4A); (2) a processus flexorius that is only weakly developed distally, with an indistinct dorsal margin, and that does not overhang to fossa oleclani (Figure 4E); and (3) a shallow fossa olecrani resulting from the 2 features mentioned above (Figure 4I). These features are developed in some individuals of *P. pelagicus* and *P. penicillatus*, but to a much lesser extent. The humeri of *P. carbo* and *P. capillatus* further differ from that of *P. perspicillatus* in a less dorsally inclined condylus dorsalis (Figure 4C).

One complete right ulna is referred to this species (Figures 2A and 3P). It is distinctively longer than the ulnae of all species examined, except for the single ulna available for *P. perspicillatus* from Bering Island (USNM O 17041), with which the Shiriya ulna agrees also in overall stoutness. The ulnae of 3 male individuals of *P. auritus* from Alaska (probably subspecies *cincinatus*) and a few individuals of *P. carbo* approach them in length, but are much more slender (Figures 2 and 5C; Table 1). In the Shiriya ulna, the dorsocranial extent of the cotyla dorsalis is relatively weakly developed distally and does not form a

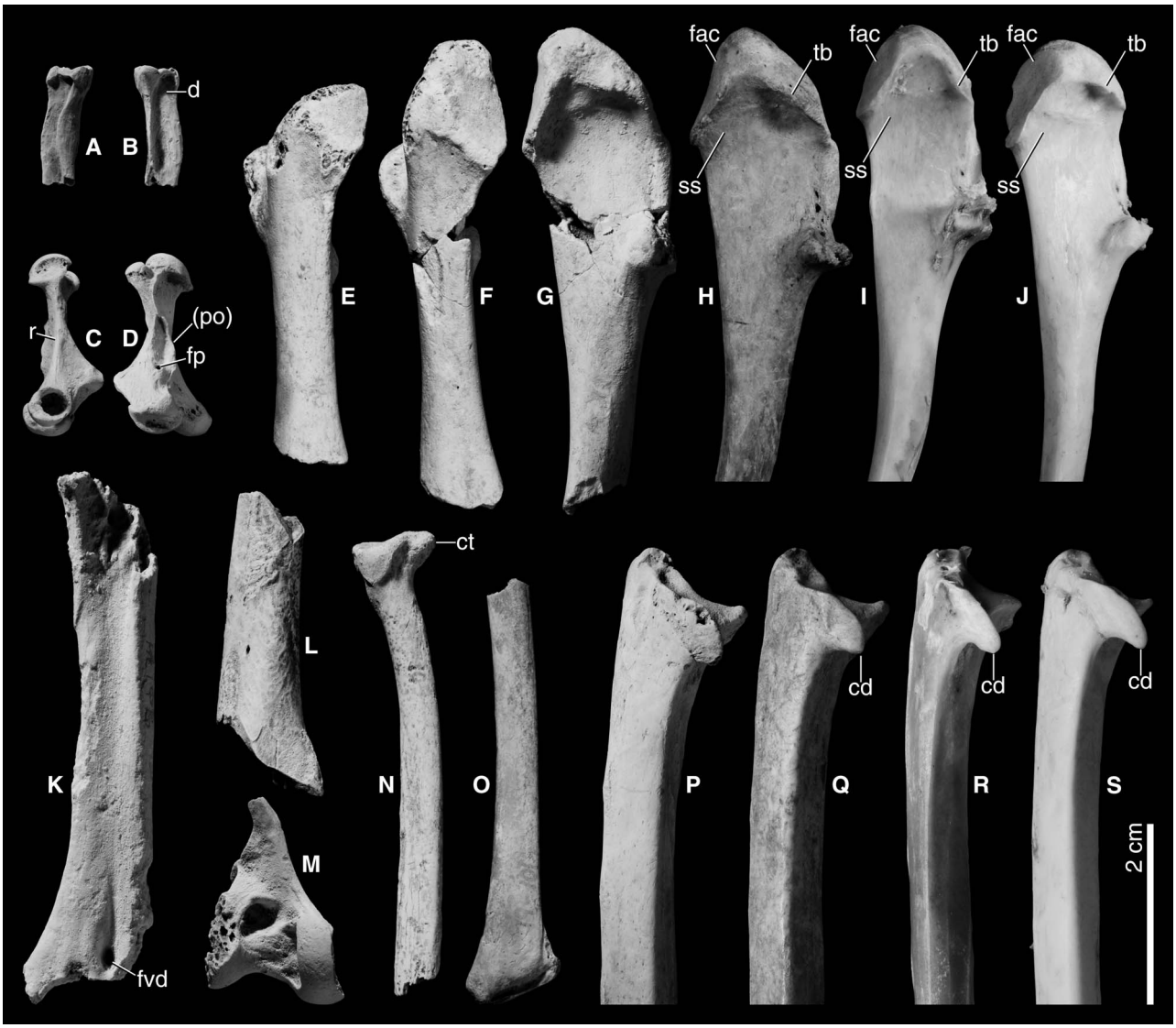

FIGURE 3. *Phalacrocorax perspicillatus* from Shiriya compared with *P. perspicillatus* from Bering Island and large individuals of other species. (**A**–**G**, **K**–**P**) *P. perspicillatus* from Shiriya: left pterygoid (NSMT PV 24194) in lateroventral (**A**) and mediodorsal (**B**) views; left quadrate (NSMT PV 24190) in lateral (**C**) and mediorostral (**D**) views; right coracoid (NSMT PV 24188) in ventral view (**E**); right coracoid (NSMT PV 24187) in ventral (**F**) and medial (**G**) views; left tarsometatarsus (NSMT PV 24189) in dorsal view (**K**); left femur (NSMT PV 24196) in caudolateral view (**L**); right tibiotarsus (NSMT PV 24193) in cranial view (**M**); right radius (NSMT PV 24195) in dorsal view (**N**); left radius (NSMT PV 19001) in cranial view (**O**); right ulna (NSMT PV 24191) in dorsal view (**P**). (**H**, **Q**) *P. perspicillatus* from Bering Island (USNM O 17041, composite skeleton): right coracoid in medial view (**H**); right ulna in dorsal view (**Q**). (**I**, **R**) modern *P. carbo sinensis* (USNM O 29696): right coracoid in medial view (**I**); right ulna in dorsal view (**R**). (**J**, **S**) modern *P. auritus* (USNM O 499388): right coracoid in medial view (**J**); right ulna in dorsal view (**S**). Shiriya fossils are coated with ammonium chloride. Abbreviations: cd = (dorsodistal extent of) cotyla dorsalis; ct = capital tuberosity; d = depression on the medial surface of the dorsal wing of pterygoid (see text); fac = facies articularis clavicularis; fp = foramen pneumaticum; fvd = foramen vasculare distale; (po) = broken base of processus orbitalis; r = ridge on the lateral margin of quadrate (see text); ss = sulcus supracoracoideus; tb = tuberculum brachiale.

prominently hooked protuberance distal to it, agreeing with *P. perspicillatus* (Figure 3P, 3Q). This state is observed in some individuals of *P. pelagicus* and most of *P. penicillatus*, but not in the other species examined, including *P. carbo*, *P. capillatus*, *P. auritus*, and *P. urile*. In the Shiriya ulna, the impressio m. brachialis is well developed with a distinct distal margin, agreeing with *P. perspicillatus*, *P. pelagicus*, *P. urile*, and *P. penicillatus* and differing from *P. carbo*, *P. capillatus*, and *P. auritus*. The shaft of the Shiriya ulna is slightly more strongly curved than the ulna of *P. perspicillatus* from Bering Island (Figure 2A, 2B).

TABLE 1. Measurements (mm) of *Phalacrocorax perspicillatus* from Shiriya compared with modern taxa and subfossil bones of *P. perspicillatus* from Bering Island. Abbreviations: D = depth, GDB = greatest distal breadth, W = width. Terms are defined in the text.

Elements	*P. perspicillatus* (Shiriya)	*P. perspicillatus* (Bering Island)			*P. capillatus* (modern)			*P. carbo* sspp. (modern)			*P. auritus cincinatus* (modern, 3 ♂♂)			*P. auritus* other sspp. (modern)		
		n	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*	Range	Mean	*n*	Range	Mean
Quadrate																
Height	20.3	0	–	–	10	17.4–19.4	18.5	15	16.0–19.1	17.6	3	19.0–20.5	19.7	11	14.9–17.4	16.3
Ventral W	13.0	0	–	–	10	11.0–12.6	12.0	33	9.8–13.4	11.3	3	11.9–13.0	12.5	20	9.8–12.1	10.8
Coracoid																
Shaft W	6.3, 6.6	2	5.6, 6.0	–	25	4.8–6.9	6.0	48	4.5–7.1	5.4	3	6.4–6.6	6.5	16	4.6–6.1	5.1
Shaft D	8.4, 8.2	2	7.9, 9.1	–	25	6.4–8.5	7.5	48	5.3–8.2	6.9	3	7.2–8.9	7.9	16	5.2–7.4	6.4
Humerus																
Shaft W	10.7, 11.0	4	10.5–11.6	10.9	24	8.4–10.2	9.3	42	7.7–11.1	9.5	3	10.2–10.9	10.5	1	9.5	–
Shaft D	7.9, 8.2	4	7.5–8.1	7.8	24	6.4–7.9	7.1	42	6.1–8.5	7.1	3	7.7–8.7	8.1	1	7.4	–
Distal W	18.1, 17.5	4	17.1–19.0	18.1	25	14.7–17.0	16.0	46	13.6–17.4	15.9	3	17.2–17.7	17.5	16	14.4–16.5	15.5
Distal D	13.5, 14.5	4	13.9–14.4	14.1	25	11.1–12.8	12.0	46	10.8–13.8	12.0	3	13.4–13.5	13.5	16	11.1–13.0	11.8
GDB	c. 20.6, 19.8	4	21.0–22.2	21.4	24	16.7–19.7	18.2	42	16.2–20.9	18.4	3	20.0–20.9	20.5	1	19.1	–
Ulna																
Length	195.0	1	189.2	–	28	154.2–176.9	164.1	46	153.8–184.1	166.2	3	174.2–189.1	179.8	16	150.5–173.0	159.5
Proximal W	16.8	1	16.3	–	28	12.5–14.4	13.4	47	11.9–15.3	13.3	3	14.6–15.2	15.0	16	11.9–14.4	12.9
Proximal D	14.6	1	14.4	–	26	11.0–12.7	11.8	47	10.4–12.9	11.7	3	12.4–13.2	12.9	16	10.5–12.2	11.2
Midshaft W	8.2	1	8.0	–	28	6.0–7.0	6.6	47	5.5–7.5	6.5	3	7.0–7.2	7.1	16	5.3–6.8	6.2
Midshaft D	8.1	1	7.8	–	28	5.3–6.8	6.2	47	5.3–7.0	6.2	3	6.9–7.2	7.0	16	5.3–6.6	6.0
Distal W	11.1	1	11.2	–	28	8.8–11.1	9.7	46	8.3–11.1	9.6	3	9.8–10.4	10.1	16	8.2–10.6	9.1
Distal D	11.1	1	10.3	–	26	8.0–9.8	8.9	45	8.0–10.1	9.0	3	10.0–10.8	10.4	16	8.0–9.8	8.7
Radius																
Proximal W	7.4	0	–	–	25	5.9–7.1	6.5	45	5.7–7.7	6.7	3	7.4–7.8	7.6	16	6.1–7.5	6.4
Distal W	11.3	0	–	–	25	9.2–10.6	9.9	44	8.8–11.0	9.7	3	10.3–11.2	10.8	16	9.0–10.2	9.6
Femur																
Midshaft W	8.3	1	8.8	–	33	6.4–7.9	7.2	56	6.1–8.1	7.0	3	7.5–8.3	7.7	16	6.3–7.5	6.8
Midshaft D	9.9	1	10.7	–	33	7.9–9.9	8.9	56	7.2–10.1	8.6	3	9.6–10.8	10.0	16	7.9–9.6	8.5
Tibiotarsus																
Distal D	14.1	8	13.7–15.5	14.5	27	12.0–13.6	12.8	49	10.8–15.1	12.2	0	–	–	16	11.2–13.8	12.0
Tarsometatarsus																
Midshaft W	8.4	9	7.5–8.8	8.2	27	6.0–7.5	6.8	49	5.2–7.2	6.3	0	–	–	16	5.8–7.1	6.3
Midshaft D	6.7	9	5.4–6.3	5.9	27	5.1–6.6	5.9	49	4.5–6.2	5.3	0	–	–	16	5.2–5.9	5.5

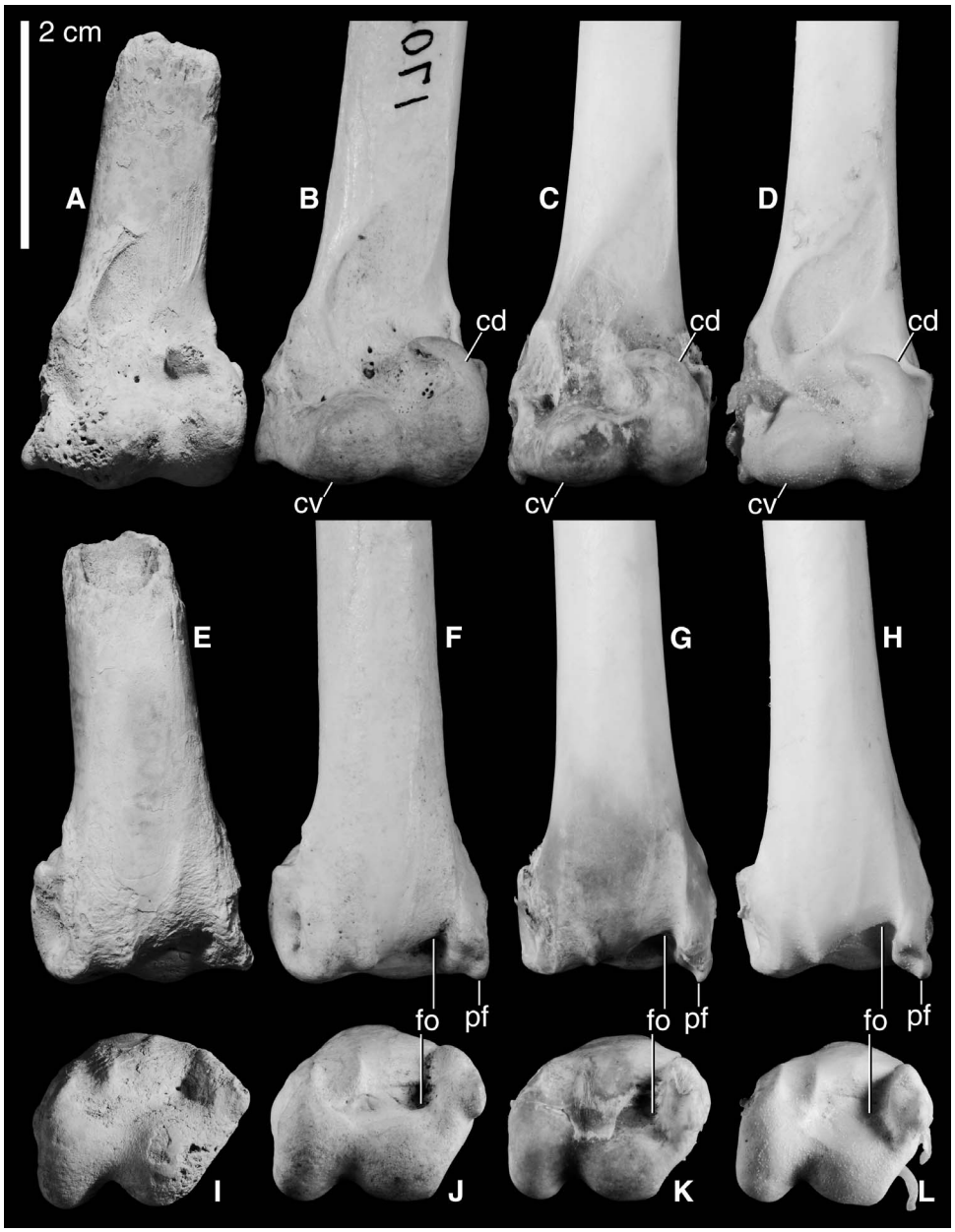

FIGURE 4. Humerus of *Phalacrocorax perspicillatus* from Shiriya compared with those of *P. perspicillatus* from Bering Island and large individuals of other species. (**A**, **E**, **I**) *P. perspicillatus* from Shiriya (NSMT PV 19000). (**B**, **F**, **J**) *P. perspicillatus* from Bering Island (USNM O 17041). (**C**, **G**, **K**) Modern *P. carbo sinensis* (USNM O 29696). (**D**, **H**, **L**) Modern *P. auritus* (USNM O 499388). Left humerus (**A**, **E**, **I**) and right humeri reversed for comparison (**B**–**D**, **F**–**H**, **J**–**L**) in cranial (**A**–**D**), caudal (**E**–**H**), and distal (**I**–**L**) views. Shiriya fossil is coated with ammonium chloride. Abbreviations: cd = condylus dorsalis; cv = condylus ventralis; fo = fossa olecrani; pf = processus flexorius.

One pterygoid preserving the caudal one-half (Figure 3A, 3B), one quadrate lacking the processus orbitalis (Figure 3C, 3D), one proximal and one distal end of radius (Figure 3N, 3O), one pelvic fragment preserving a part of acetabulum, one femoral shaft (Figure 3L), one distal end of tibiotarsus (Figure 3M), and one worn tarsometatarsal shaft (Figure 3K) are tentatively referred to this species. Because some of these elements (pterygoid, quadrate, and radius) are not known for *P. perspicillatus*, the referral to this species is based mainly on their large size. A prominent feature of the pterygoid is the presence of a distinctive depression on the medial surface of the dorsal wing, which is not so clearly observed in any other species examined. In the quadrate, the corpus ossis quadrati is rather slender compared to *P. carbo*, *P. capillatus*, or *P. auritus*, possibly as a result of reduced pneumaticity; in

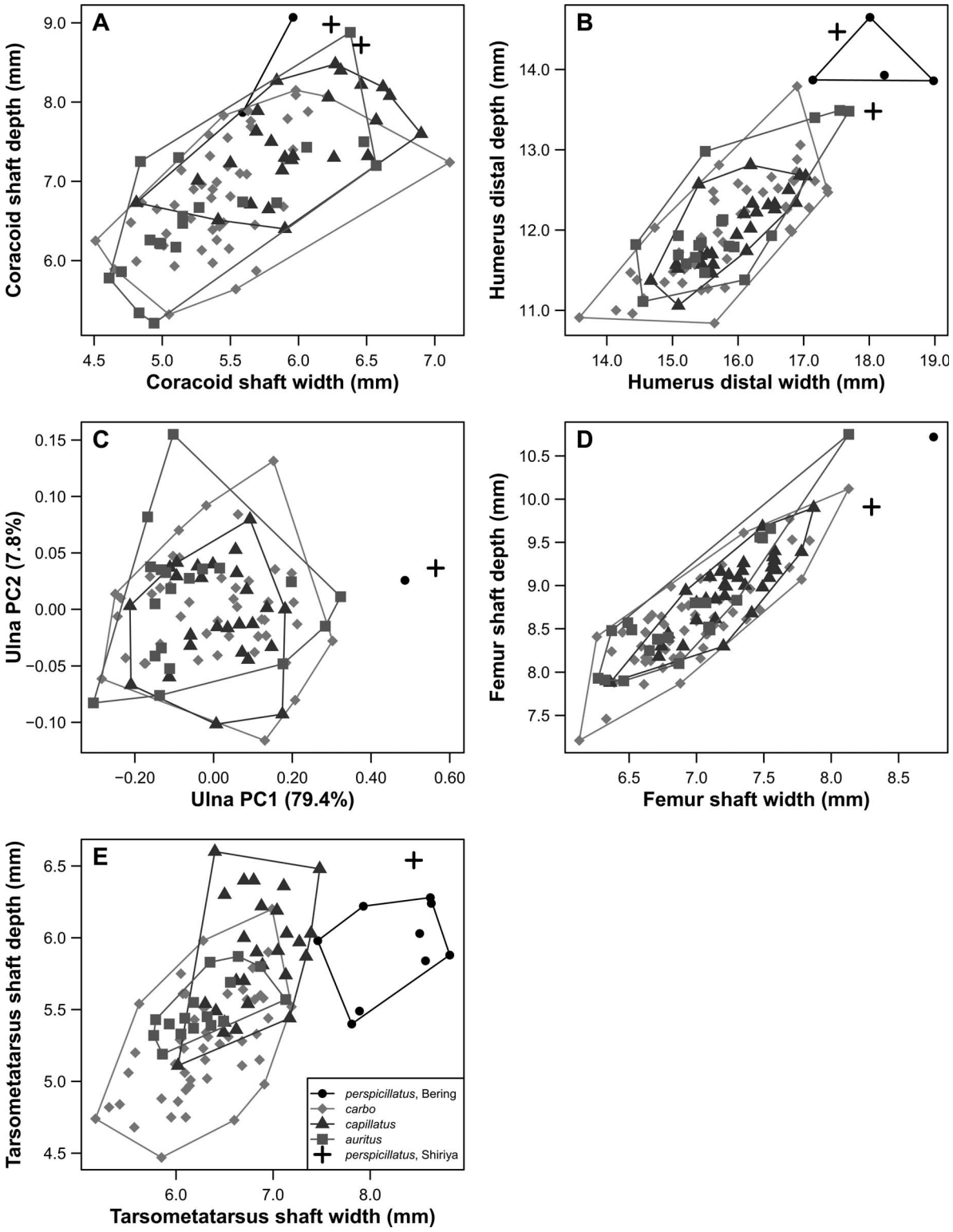

FIGURE 5. Scatter plots of individual measurements and principal component (PC) scores. (**A**) Coracoidal shaft measurements. (**B**) Distal humeral measurements. (**C**) PC scores based on 7 ulnar measurements (for details of the analysis, see Appendix B). (**D**) Femoral measurements. (**E**) Tarsometatarsal measurements. Legend: black circle = *P. perspicillatus* from Bering Island (USNM O 17041 and 19417); diamond = modern *P. carbo* from various localities; triangle = modern *P. capillatus*; square = modern *P. auritus*; plus sign = *P. perspicillatus* from Shiriya.

those 3 species, the foramen pneumaticum is a large opening on the medial side of the body, whereas in the Shiriya quadrate the foramen is only a minute opening (Figure 3D) as in some individuals of *P. penicillatus*, where some intraspecific variation is observed in the development of the foramen. On the other hand, the foramen pneumaticum is much smaller or completely absent in *P. pelagicus* and *P. urile*. The Shiriya quadrate further differs from those of *P. carbo*, *P. capillatus*, and *P. auritus* and agrees with *P. pelagicus* and *P. urile*, in a sharp lateral margin of the body that forms a distinct ridge extending from the capitulum squamosum to the condylus lateralis, and a weakly developed condylus caudalis (Figure 3C); in the former 3 species, the lateral margin is rather round and wide, forming only a blunt ridge, and the condyle is well developed ventrally and poses a bulbous outline in caudal view. The quadrate of *P. penicillatus* shows some variation in these features, but the ridge on the lateral margin is always present. In addition, the Shiriya quadrate shows a unique feature in the processus oticus; the capitulum oticum and capitulum squamosum are widely separated, and the caudal surface between the 2 capituli is deeply excavated. The proximal radius differs from those of *P. carbo* and *P. penicillatus* in a capital tuberosity that is not elongated proximodistally or displaced distally from the proximal end. The Shiriya tarsometatarsus has a small foramen vasculare distale, as in modern *P. perspicillatus*, *P. pelagicus*, and *P. urile*.

Remarks. The fossil record of the Phalacrocoracidae is rather scattered (Olson 1985, Emslie 1995), but only a few fossil species seem to compare in size to *P. perspicillatus*, all of which can be distinguished from the Shiriya material. *Phalacrocorax macropus* (Cope, 1878) is known from several elements from the upper Pleistocene of Oregon and California, USA (Shufeldt 1892, Howard 1946, Jehl 1967, Jefferson 1985). The 2 coracoids of *P. macropus* examined (USNM VP 8274 and 8275) are as large as that of *P. perspicillatus* but are qualitatively similar to *P. auritus* as described by Howard (1946), particularly in the broadness of the area on the ventral surface of the processus acrocoracoideus lateral to the facies articularis clavicularis. Another large species, *P. rogersi* Howard, 1932, is known from a coracoid from the Pliocene of California. According to the original description and illustration (Howard 1932), this species differs from *P. perspicillatus* in the facies articularis clavicularis and tuberculum brachiale that are not strongly developed medially. *Phalacrocorax idahensis* (Marsh, 1870) from the Pliocene and lower Pleistocene of North America (Wetmore 1933, Becker 1986) has a more slender ulna, according to published dimensions (Murray 1970, Emslie 1998).

The only phylogenetic hypothesis that included *P. perspicillatus* is a morphological tree of Siegel-Causey (1988), in which the species was placed within the clade comprising *P. perspicillatus*, *P. penicillatus*, *P. harrisi*, *P. fuscescens*, and *P. neglectus*. The validity of characters used by Siegel-Causey (1988) has been criticized by subsequent authors (Rohwer et al. 2000, Olson 2005), and the topology is largely incongruent with recent molecular phylogenies (e.g., Holland et al. 2010, Kennedy and Spencer 2014). In regard to the species examined (see Appendix A), osteological features of *P. perspicillatus* observed in the present study are most similar to those of *P. penicillatus*, *P. pelagicus*, and *P. urile*, which comprise a clade in the molecular tree presented by Kennedy and Spencer (2014). Nevertheless, the polarities and phylogenetic consistencies of the osteological characters are uncertain; thus, their phylogenetic or taxonomic usefulness would require additional evaluation, if they are to be used above the species level of identification.

DISCUSSION

Four *Phalacrocorax* species occur in Japan and nearby seas today: *P. pelagicus* (subspecies *pelagicus*; Pelagic Cormorant) and *P. urile* (Red-faced Cormorant), which occur in northern Japan and are pelagic in habit; *P. carbo* (subspecies *hanedae*, whose validity has been considered doubtful by many authors), a common freshwater species; and *P. capillatus*, a coastal species. Although some specimens described here were once referred to *P. capillatus* by Hasegawa et al. (1988), they can be distinguished from all 4 of these species by distinctly larger size and qualitative features as described above. Although there is a marked geographic variation in size in *P. carbo* (see, e.g., Johnsgard 1993), examination of specimens from various localities in this study confirmed that the species shows little qualitative variation in the osteological features mentioned above; thus, they can be differentiated consistently from *P. perspicillatus*. Another species of possible concern is *P. auritus*, which is distributed over North America and the Aleutian Islands. The northern race of this species distributed in Alaska and the Aleutians (*P. a. cincinatus*) is clearly larger than other races (Johnsgard 1993), and underappreciation of the geographic variation has led a previous study (Siegel-Causey et al. 1991) to an erroneous identification of an archeological specimen of this species as *P. perspicillatus* (see Olson 2005). In the present study, 3 male individuals of *P. auritus* from Alaska were examined and indeed were found to approach *P. perspicillatus* in some dimensions as pointed out by Olson (2005) (Table 1). Nevertheless, bones of these individuals could be distinguished from those of *P. perspicillatus* in overall slenderness, as well as the qualitative features mentioned above. As far as observed in the available materials, there are few qualitative differences between the fossils from Shiriya described here and the subfossil bones of *P. perspicillatus* from the Bering

Island. There are several apparently unique osteological features shared between the Shiriya and Bering materials (see above). Hence, it appears most certain that the specimens from Shiriya described in this study represent *P. perspicillatus*, rather than geographic or temporal variants of other modern species.

The occurrence of *P. perspicillatus* from the upper Pleistocene (MIS 5e) of Shiriya is the first definitive record of this species outside Bering Island, as well as the first pre-Holocene fossil record of the species, expanding the known geographic and temporal ranges of the species by ~2,400 km and ~120,000 yr, respectively. It indicates that this supposedly island-endemic species was once not restricted to Bering Island; it had a larger geographic range or underwent a considerable distributional shift in the Quaternary North Pacific. Either way, the historical population of this species on Bering Island is best considered a relict.

The occurrence of *P. perspicillatus* from the Pleistocene of Japan is not totally erratic, given that many other seabirds and marine mammals are shared between middle and high latitudes in the western North Pacific. Examples include seaducks (e.g., *Clangula hyemalis*, *Melanitta* spp.), other cormorants (*P. pelagicus* and *P. urile*), and alcids (*Fratercula* spp., *Aethia* spp., *Synthliboramphus antiquus*). The entire Shiriya paleoavifauna is currently under revision by the authors, after which the biogeographic and ecological implications of the present study can be discussed in more detail.

Interestingly, the relict pattern of *P. perspicillatus* parallels that of another large marine vertebrate, *Hydrodamalis gigas* (Steller's sea cow), in the North Pacific. The sea cow was once thought to have had been restricted to the Commander Islands and western Aleutian Islands before it was driven to extinction in the 18th century by overexploitation (Mattioli and Domning 2006, Domning et al. 2007), although there is a Holocene subfossil record from St. Lawrence Island in the Bering Sea (Crerar et al. 2014). Fossils of this species are also known from the upper Pleistocene of California (Jones 1967) and at least 2 middle Pleistocene localities in Japan (Shinohara et al. 1985, Furusawa and Kohno 1994), indicating that the species has undergone a range contraction since the Pleistocene. It is tempting to speculate that the parallel range contractions or shifts of *P. perspicillatus* and *H. gigas* were partly driven by a common factor, such as climate change or indirect effects of community structure change, the latter of which has been suggested to have played a role in the recent decline of *H. gigas* (Anderson 1995, Estes et al. 2016).

The local disappearance of *P. perspicillatus* from Shiriya may be due, in part, to oceanographic changes since the Late Pleistocene. An analysis of radiolarian assemblages from a seafloor sediment core by Matsuzaki et al. (2014) showed that the oceanic productivity around Shiriya was higher in the age of the Shiriya local fauna, MISs 9–5e, than in the preceding period. It is conceivable that the population of *P. perspicillatus* was sustained by the elevated productivity in that age. However, changes in oceanographic conditions in the subsequent Last Glacial Maximum resulted in a drop of oceanic productivity (Kuroyanagi et al. 2006, Minoshima et al. 2007, Matsuzaki et al. 2014), which would have seriously affected the population of *P. perspicillatus* in this area. The effect of this event may not be limited to this species; other unique components of the Shiriya paleoavifauna, including a flightless duck (*Shiriyanetta hasegawai*) and a large murre (*Uria onoi*), became extinct since the Late Pleistocene (Watanabe and Matsuoka 2015, Watanabe et al. 2016). Although this is an admittedly simplistic scenario that needs further evaluation, it is conceivable that such local oceanographic changes have affected population dynamics of such large-bodied, and hence slowly breeding, seabirds in many local communities worldwide since the Late Pleistocene. An alternative scenario for this specific case is that the species were driven to (local) extirpation by human overexploitation. Nevertheless, at present, no archeological remains of these species have been recorded from Japan. Revision of archeological records in light of the present finding, as well as an ongoing excavation of an archeological site in the Shiriya area (Nara et al. 2015), may shed new light on the local extinction events.

Although the direct cause of the extinction of *P. perspicillatus* was probably overexploitation by humans, the whole picture may be more complex, as is the case for recent extinctions of some other large-bodied seabirds (Jones et al. 2008, Rawlence et al. 2017). It is possible that the cormorant species had already decreased its range when it was first scientifically discovered in the 18th century, or even before the first contact with humans in prehistoric times.

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APPENDIX A

Comparative Material Examined

Specimens are listed by species or subspecies and by geographic region, with sex composition in parentheses (m = male, f = female, u = unsexed).

Phalacrocorax melanoleucos: Australia, MVZ 143272–143277 (1 m, 5 f). *P. gaimardi*: Peru, MVZ 157988 (m). *P. atriceps bransfieldensis*: Antarctica, UWBM 37903–37905 (3 m). *P. auritus auritus*: New York, MVZ 49570–49572 and 151571–151575 (8 u). *P. auritus albociliatus*: Nevada, MVZ 78986, 80617, and USNM O 499388 (1 m, 1 f, 1 u); California, MVZ 73105, 77237, 79038, 151570, 175973, 179932, and 182794 (3 m, 3 f, 1 u). *P. auritus cincinatus*: Alaska, UWBM 48555, 48615, and 52044 (3 m). *P. brasilianus mexicanus*: Guatemala, MVZ 46167 (m); El Salbador, MVZ 85508 (f). *P. harrisi*: Galapagos, MVZ 134079 and 140913 (1 m, 1 f). *P. penicillatus*: Washington, UWBM 53584 and 78817 (1 m, 1 f); Oregon, UWBM 81707 and 81732 (1 m, 1 f); California, MVZ 41146, 44108, 46808, 46809, 49385–49388, 49409, 70622, 70623, 151576–151578, 151580–151583, 157664–157667, 175975, and 175976 (4 m, 9 f, 11 u). *P. pelagicus pelagicus*: Alaska, MVZ 28976, 60287, 60288, 62420, 68389, UWBM 18613, 18614, 40527, 48614, 50578, 51968, 52103, 52109, 52110, 52112, 52115, 52120, 52121, 52123, 52126, 52128, 78767, 78769–78773 (5 m, 18 f, 4 u, including 2 paratypes of "*Stictocarbo kenyoni*"); Japan, EP 95, MVZ 124050 NSMT AS 534, and 1196, YIO 64939, 70521 (2 m, 4 u); *P. p. resplendens*: Washington, UWBM 78804, 78809–78812, 78814, 78823, and 78826 (2 m, 5 f, 1 u); California, MVZ, 19088–19090, 51452, and 175977 (2 m, 1 f, 2 u). *P. urile*: Alaska, MVZ 154266–154269, UWBM 48618, 48619, 50610–50612, 51948, 51950, 51951, 51953, 51955, 51993, 52083, 52084, 52086, 52089–52094, 52106, and 52017 (12 m, 14 f). *P. perspicillatus*: Bering Island, USNM O 17041 and 19417 (composites of isolated midden bones). *P. carbo carbo*: Britain, MVZ 166155 and USNM O 18851 (2 u); Iceland, USNM O 292350 (u); Massachusetts, USNM O 553884 (m). *P. carbo sinensis*: Netherlands, USNM O 614123 and 614239 (2 m); Krasnodar Krai, Russia, UWBM 61351 (m); Kazakhstan, UWBM 46258 (f); Mongolia, UWBM 59908 (m); China, USNM O 291660, 292696, and 292758 (2 f, 1 u). *P. carbo hanedae*: Japan, EP 191, 192, 195, 198, 213, 257, NSMT AS 1068, 1120, 1144, 1274, NSMT PV A132, A535, A536, USNM O 641776, 641780, 641878, 641886, YIO 60754, 64423, 65125 (5 m, 2 f, 13 u). *P. carbo novaehollandiae*: Australia, MVZ 143257–143260 and UWBM 62870 (5 f); New Zealand, USNM O 560236 (f). *P. carbo lucidus*: South Africa, USNM O 558372 and 558373 (1 m, 1 f); Kenya, 431685 (f). *P. capillatus*: Japan, EP 43, 111, HUMNH 60468, MVZ 124049, NSMT AS 537, 1308,YIO 65223, 65438 (1 m, 7 u). *P. capensis*: South Africa, USNM O 558374 (m). *P. nigrogularis*: EP 280 (u, locality unknown). *P. sulcirostris*: Australia, MVZ 143250–143256 (1m, 6 f). *P. varius hypoleucos*: Australia, MVZ 143261–143271 and 155696 (10 m, 2 f). *P. punctatus*: New Zealand, MVZ 164582 (u). *P. macropus*: Christmas Lake, Oregon, USNM VP 8274 and 8275 (fossils).

APPENDIX B

Principal component analysis was conducted to obtain an ordination based on 7 ulnar measurements (Figure 5C). The analysis was based on the covariance matrix of natural log-transformed variables (Appendix Table 2). Although the point for *P. perspicillatus* from Shiriya was plotted a posteriori in Figure 5C, similar results and ordination were obtained even when it was included a priori in analysis.

APPENDIX TABLE 2. Summary of principal component (PC) analysis based on 7 ulnar measurements (Figure 5C). Eigenvectors, corresponding eigenvalues and proportion of variance explained (PVE), and PC loadings are shown for the first 2 PCs, as well as the total mean vector (Mean). The sample includes 19 individual of *Phalacrocorax auritus* (including 3 *cincinatus*), 44 *P. carbo*, 26 *P. capillatus*, and 1 *P. perspicillatus* from Bering Island (total $n = 90$).

	Eigenvectors			PC loadings	
Variable	PC1	PC2	Mean	PC1	PC2
Length	0.2807	−0.0806	5.1067	0.8777	−0.0789
Proximal width	0.3962	−0.0959	2.5909	0.9417	−0.0713
Proximal depth	0.3721	−0.2144	2.4565	0.9295	−0.1676
W midshaft	0.4201	0.4767	1.8703	0.8926	0.3170
D midshaft	0.4302	0.5621	1.8250	0.8959	0.3664
Distal width	0.3846	−0.5885	2.2577	0.8352	−0.4001
Distal depth	0.3409	−0.2211	2.1935	0.8624	−0.1751
Eigenvalue	0.1525	0.0477			
PVE	79.4%	7.8%			